XIV. *The Colour-groups of the* Hawaiian Wasps, *etc.* By R. C. L. Perkins, D.Sc., M.A., Jesus College, Oxford.

[Read October 16th, 1912.]

[In the autumn of 1911 I had the opportunity of discussing the subject of this memoir with Dr. Perkins during a too brief visit paid by him to Oxford. The discussion, thus begun, was continued with some energy on both sides, in a correspondence which only ended when Dr. Perkins sailed for Honolulu in November 1911. In the course of our correspondence he sent me a manuscript note-book, written about 1907–8, as part of his Introduction to the ' Fauna Hawaiiensis," now in the press. The facts and inferences concerning the present condition and past history of these Colour-groups seemed to me of such fundamental importance in the study of mimicry and indeed of evolution, that it appeared most desirable to publish the supplementary information and the further conclusions scattered through the letters. Dr. Perkins consented, and the following paper is the result. In order to understand the nature of the discussion, it has been necessary to quote passages and sometimes consecutive paragraphs from the note-book which will soon be published as the Introduction. For this free use of the manuscript I received the kind consent of Dr. David Sharp, F.R.S., Editor of the "Fauna Hawaiiensis." It must be clearly understood that the quotations are from the manuscript and not from the printed pages of the Introduction itself, and that some slight difference between the two accounts is to be looked for, owing to Dr. Perkins' final revision for the press. I have limited these quotations to the minimum quantity necessary to preserve continuity and to explain the letters, bearing in mind the inconvenience of printing the same passages twice over in two publications. No quotations from the note-book appear later than page 690, and in all the earlier part of the paper, where they occupy a large proportion of the pages, they are clearly discriminated from passages extracted from the letters, the latter being

between inverted commas and dated. I have not necessarily kept the extracts from the note-book in their original order and have ventured to condense certain parts. Beyond the point where extracts from the note-book cease, the quotations from the correspondence are no longer placed between quotation marks and are dated at the head instead of at the foot as in the earlier parts of the paper. In the concluding pages the passages are grouped under three separate heads. The few slight additions of my own are placed between the square brackets. Species quoted without an author's name were described by Dr. Perkins himself.—E. B. Poulton.]

Eumenidae.

[This family is considered first because of the number of the Hawaiian species and the dominant position taken by them in the Colour-groups of these islands.]

The whole of the species, to the number of 102, belong to the almost ubiquitous genus *Odynerus, sensu latiori.* From this interesting complex I have split off three small groups of species and considered them as distinct genera, as indeed they are, although they appear to be derivations of the same stock as the Hawaiian *Odynerus* proper. The Hawaiian Eumenids are, I now think, clearly descendants of two quite distinct forms of original immigrants, one of which, a yellow-banded form, gave rise to the bulk of the species, as well as to the endemic genera that I have separated from these, while the other has produced but four distinct species, as at present discovered, viz. *O. nigripennis,* Holmgr., and its three allies. This little group has now been traced to an Asiatic ancestor which is, I suspect, an ancient or primitive type, showing some affinity to the genus *Rhynchium,* in which *nigripennis* itself was originally placed by Holmgren.

"I have not yet identified the Oriental species (just lately discovered while mounting some insects) that is allied to the *O. nigripennis* group. It is the closest approach I know to the genus *Rhynchium,* but it is not that genus." *Nov. 13th, 1911.*

Species of *Odynerus* are almost ubiquitous throughout the islands, though some of the densest and wettest boggy forests are absolutely devoid of them. At the same time a slight change in these, made by the incursion of cattle,

is sufficient to allow of some species becoming established where previously they could not exist.

"Practically speaking, the cattle open up the dense forest, letting in sunlight and making it much drier. It is remarkable that no species of *Odynerus* should have been able to enter our densest and wettest virgin forests, because it would have found there such a vast store of (Lepidopterous) food, without other species to compete with it. Some of the bees have occupied such forests, in spite of the sun-loving habits of the group." *Nov. 13th, 1911.*

The prey of Hawaiian Eumenidae, so far as is known, consists entirely of caterpillars. On the whole it may be said that Pyralid and Microlepidopterous caterpillars are the favourite prey and that Geometridae are rarely utilised. It is most remarkable, seeing that the latter are occasionally taken (e. g. by *O. montanus*, Sm., *eucharis*, etc.), that this should occur so rarely, for the Geometrid caterpillars are so very numerous that they could be often obtained in any quantity.

In many localities at favourable seasons the number of individuals that are seen is extraordinary. On one occasion I visited a mountain gulch on Molokai nearly every day for three weeks, and I estimated that in a length of a couple of miles (below the line of forest) the population of adult wasps was at least one million. Five or six species were represented, but two or three were much more numerous than the others. I have noticed an almost similar abundance in other localities. It is probable that very few of the large number of species are really rare.

With experience and close attention in the field, it is fairly easy to discriminate between species that are exactly alike superficially, owing to indescribable differences in appearance, due to mode of flight and posture.

Only in exceptional cases do the Hawaiian Eumenidae exhibit important variation, and in very few cases is this more than of a trifling character, affecting the colour. A common variation, which occurs again and again and in the most diverse species, is the occasional assumption of a feeble yellow band or traces of such a band on the first and second abdominal segments in species which typically have an entirely black body. Examples of this are *Nesodynerus rudolphi*, Dalla Torre, *Odynerus venator*, and *O. heterochromus*, to instance only species very widely

separated in structure. Sometimes the yellow band appears only on the *ventral* surface. The phenomena are precisely identical with those observed in the *Crabronidae* (see p. 688), and, I think, are explicable in the same way. The blackness of so many Hawaiian Eumenids has been produced in the islands and the abnormal individuals are reversions to a former general condition in colouring. The Eumenids, furthermore, like the Crabronids, have retained in some species the original yellow-banded coloration.

The general tendency to blackness of the Hawaiian Aculeata, as a whole, is one of their most remarkable features. The blackness of these insects is increased by the dark colour of their wings, which, in a large number of the species, exhibits striking blue or purple reflections.

"My original paper * on colour of Hawaiian wasps was written too early to have much value. I treated only the Kauai species as conspicuous on account of the pale bands. This was an error; all the things I send as examples are conspicuous in life: they are *the* conspicuous feature among the day-flying insects in the islands and about the only one, except at special times and places." *Nov. 8th, 1911.*

The following Colour-groups—entirely different from the groups based on structure and real affinity—are distinguished in the Introduction.

On Kauai are two Colour-groups, one of which contains only two known species.

Group I. Insects with much red marking, wings shining fuscous, when spread.

O. blackburni, Kirb., and *soror*: allied species.

Group II. Black insects with two conspicuous whitish or yellow bands † on abdomen; wings dark and with conspicuous blue or purple reflections. Fourteen species of diverse structure.

"Kauai is the most northern of the forest-bearing islands, and it has by far the widest channel between it and its next neighbour—Oahu. The specific characters of its species are usually the most striking of those exhibited on any island, but it lacks representatives of many 'groups'

* Proc. Phil. Soc. Cambridge, vol. ix, Pt. VII (1897), p. 378. The examples alluded to were exhibited to the Entomological Society, May 1st, 1912 (Proceedings, pp. lvi–lxv).

† "When the insects are on the wing, these bands are clearly seen."—R. C. L. Perkins, in Proc. Phil. Soc. Cambridge, vol. ix, Pt. VII (1897), p. 378.

of species in big genera. We have found no representative so far of *Chelodynerus*, none of the '*nautarum*,' de Sauss., group of *Odynerus* (probably one of the most ancestral), and it has no peculiar structural group, so that probably the groups of *Odynerus* in the islands were already formed before the genus chanced to reach Kauai, and some have not yet reached it. This is likely to be the case from a consideration of the beetles; for the Carabid *Cyclothorax* (s. l.), now split into several genera, is unknown on Kauai, very poor on Oahu, the next island, very rich on the intermediate islands, and rather rich on Hawaii at the other extremity. This fact alone, without appealing to the geological reasons, is sufficient to disprove Lord Walsingham's conclusion that the islands were once a larger *continuous land-area.* (See also p. 697.)" *Nov. 15th, 1911.*

In Oahu are four Colour-groups, two of which (II and III) may be said to be peculiar to this island.

Group I. Black insects with dark wings, showing conspicuous blue or purple reflections.

O. nigripennis, Holmgr., *epipseustes, erro, iopteryx, montanus*, Sm., *konanus, unicus; Nesodynerus optabilis* and *rudolphi*, Dalla Torre.

Group II. Generally small species, black with shining fuscous wings: no blue reflections. In this group some species show feeble and variable pale abdominal bands, and others some red markings apparently tending to disappearance, and not conspicuous.

O. dubiosus, Sm., *threnodes, pterophaennes, waianaeanus, paludicola, paranaias; Nesodynerus oblitus* and *acyanus.*

"The differences between species of the same genus which enter different Colour-groups are well seen in *Nesodynerus.* Thus *N. rudolphi* (I) is very common and ubiquitous, frequenting both forest and open country, while *N. oblitus* (II) is also abundant, but only occurs in localities—never forests—in which the very common species of *Odynerus*, viz. *dubiosus*, etc. (II), are found." *Nov. 15th, 1911.*

Group III. Insects usually much marked with red, and the body with appressed fuscous tomentum. Wings to a large extent hyaline and with no blue reflections.

O. pseudochromus, pseudochromoides, leiodemas, homoeophanes, eucharis, oahuensis, Dalla Torre.

On one occasion all the six members of this group were taken in the same spot and on the same day.

"The species fall into three very distinct structural groups:—(1) *O. oahuensis*: isolated structurally and in habits: common in all suitable localities, but less so than *O. pseudochromus*: affinity with other Hawaiian *Odynerus* is not clear, but requires far more study; (2) *O. pseudochromus, pseudochromoides, leiodemas*: allied species, the first two ubiquitous and common in their proper localities: the third is probably generally to be found with them, but is much less numerous; (3) *O. eucharis, homoeophanes*: allied species, of which one is found with species of the structural group (2) in some localities, the other with them in other localities. They are probably always relatively rare." *Nov. 15th, 1911.*

Group IV. Insects with usually two pale abdominal bands, the wings more or less infuscate and with blue reflections, body generally with pale tomentum.

O. xerophilus, nautarum, de Sauss., *acoelogaster*; *Pseudopterocheilus relictus.**

* [I was particularly anxious to see the members of Colour-groups which had been captured at the same time and place, in order to be able to estimate the relative numbers and obtain conclusive evidence as to the predominant species. Dr. Perkins very kindly collected for me on three occasions the specimens which are tabulated in the following extract from his letter, written May 20th, 1912, from Honolulu. The captures of each date are kept together in the Hope Department, where they may be studied at any time. They were exhibited, in illustration of Dr. Perkins' paper, at the Second Entomological Congress at Oxford during the past summer.]

I have been out in the country on three occasions lately to catch *Odynerus*, and had Kershaw to help me. It is a bad season on the lowlands, as we have had no winter rains and the country most favourable for Hymenoptera is parched up. It is interesting to see what is dominant under these conditions.

On the first day (April 26th, 1912, Makiki, Oahu, below 400 ft.) caught only one species, *O. nigripennis* (38 specimens), but I saw one individual either of *Nesodynerus rudolphi* or *Od. montanus*.

On the second day (May 3rd, lowlands near coast, east of Honolulu) we caught of the same all-black, blue-winged Group I:—

O. nigripennis (21)
O. montanus (1)
O. iopteryx (2)
Nesodynerus rudolphi (6)
} 3 structural groups in these 4 species!

Of the white-banded Group IV:—
O. acoelogaster (10).
O. nautarum (1).
Ps. relictus (1).

On Maui, Molokai and Lanai, the fauna of each of which is largely the same, we have three groups :—

Group I. Identical with I on Oahu.

O. nigripennis, Holmgr., *purpurifer*, *instabilis*, *ecostatus*, *laevisulcatus*, *camelinus*, *brevicostatus*, *aprepes*, *lanaiensis*, *konanus*; *Nesodynerus eupteryx*, *paractias*; *Pseudopterocheilus congruus*, Sm.; *Chelodynerus chelifer*.

Group II. Identical with IV on Oahu.

O. molokaiensis, *sociabilis*, *smithii*, Dalla Torre, *insulicola*, Blackb., *nubicola*, *nivicola*.

Of the small shining-fuscous winged Group II :—
O. dubiosus (7).
O. threnodes (3).
Nesoprosopis assimulans (2).

Had it been a good season, of I there would have been many more *montanus*, otherwise proportion as above.

Of IV we should have found *O. xerophilus* numerous locally and *Pseudopterocheilus relictus* abundant, otherwise proportion as we found above.

Of II we should have also found *Nesodynerus oblitus*, local, not general like the two above-named species of this group.

The third day (May 10th, Palolo) we collected at 1200–1500 ft. in forest.

Of the curious clear-winged Oahu Group III, with dull red marks we got only :—

O. pseudochromus (16).
O. oahuensis (3).

On a good day we might have found the closely allied *O. pseudochromoides* nearly as common as *pseudochromus*, with *one or two individuals* each of the three rare species, *O. eucharis*, *leiodemas*, and one other closely allied to *eucharis*, viz. *homoeophanes*. All these occur in the very spot where we collected.

Of Group I we got *O. rudolphi* (10), *O. nigripennis* (4), and *O. montanus* (1) : also *Hylocrabro tumidoventris* (5), *Xenocrabro unicolor*, Sm. (1).

Group I was also represented by the Ichneumonid, *Echthromorpha fuscator* (*maculipennis*, Holmgr.) (5).

The little endemic flycatcher, *Chasiempis*, was fairly common, young and old, and as tame as usual, but was clearly not paying any attention to Hymenoptera. The chief interest to me of the whole collection is the evidence as to what species are most abundant under circumstances unfavourable for Hymenoptera. From long experience I know exactly what one would, or might expect to get under favourable circumstances.

Group III. Insects with red thoracic or abdominal markings, or both, the wings dark and with blue reflections.

O. frater, Dalla Torre, *monas, cephalostictus, naiadum, tempe, dryas, potamophilus, microdemas, monobius, erythrostactes, montivagus, sandwichensis*, de Sauss., *petrobius, deinogaster, homocogaster.*

On Hawaii there is a general tendency of the above three groups to become fused into one large group, all representing I on Oahu, and on Maui, Molokai and Lanai. *O. obscurepunctatus*, Blackb., and *rubropustulatus*, Blackb., and one or two others may be recognised as obscure members of Group III, of Maui, etc. *O. newelli, sociabilis*, and *scoriaceus* represent II.*

Speaking generally of these groups, I find that in the field, the members of each are easily enough distinguished. There are, as might be expected, some cases of species that are intermediate in appearance and might be placed in either of two groups, but these are very few. On Kauai Group II stands out remarkably from all others, since nearly all the Kauai species belong to it, while it is only approached in appearance by a few species in Group IV on Oahu. The tendency of the species to become red-marked on the three intermediate islands (Maui, etc.) is very

* [At this point it is convenient to print Dr. Perkins' comments on the abstract of this paper and the lists of specimens sent by him for exhibition when it was read (Proceedings 1912, pp. lvi–lxv). Dr. Perkins arranged the specimens and wrote the lists in the midst of the preparations for his departure from this country, and he had no opportunity of revising the MSS. On his return to England he wrote, September 17, 1912, stating that my footnotes on pp. lviii, lix are correct, and that *N. pubescens*, var. in B (p. lviii), and *N. fusci-pennis* in E (p. lix) should be transposed. He furthermore explained that the common typical *N. pubescens* placed in E (lix) does not in reality fit into any group on Hawaii. Dr. Perkins wrote :—

"I suppose I sent a specimen for comparison with the rare blue-winged form, which we should expect to be dominant, and if selective processes were going on now, would surely become so, this being a grand chance for natural selection to work upon. The rare variety is the one that fits the colour-scheme of Hawaii, the very abundant typical form does not."

Concerning *O. molokaiensis*, referred to in the footnote on p. lix, Dr. Perkins remarked that "the female never has bands and is a perfect representative of the dominant Colour-group (E = I). *O. molokaiensis* male may have two fairly good pale bands (as in II of Molokai, etc. = IV. of Oahu), or one may be entirely obliterated and the other faint."]

striking, nearly half the known species being so coloured. Group IV on Oahu (= II of Maui, etc.) is not very clearly marked off from its Group I, when the insects are seen in flight, but, as they usually have a characteristic grey or hoary appearance, they may be kept apart, especially as they represent species mostly peculiar to open country or open spaces in forest country. When their representatives on Hawaii are considered, they become much less distinct from those representing Group I on that island.

Groups II and III on Oahu are peculiar to itself, the dull red markings, clear wings and body clothing of the former giving them, dead or alive, an appearance unlike anything else, and the shining fuscous wings of the latter rendering these equally unmistakable.

In a few cases, isolated species have been found on islands, where they ill accord with the groups there represented, but one cannot overlook the probability of these being recent immigrants. Thus *O. frater*, Dalla Torre, a widely distributed species, has been found very rarely on Oahu, where it does not fit into any Colour-group, as it does on Maui, where it abounds. Excepting on Kauai, the Group I of Oahu is well represented on every island, besides tending to absorb all others on Hawaii, so that nearly half the known species of the wasps may be referred to it. The dominance of this group increases the blackness of our series, for it contains species almost or entirely black and with dark iridescent wings; and, when other groups of Hymenoptera are considered, is swelled by species of bees, of fossorial wasps, and even of parasitic Ichneumonoids.

"In these associations of Aculeates, the Eumenidae are probably dominant, although both the Fossores and bees are extremely ancient. In the Crabronidae several genera have been evolved probably from a single ancient immigrant species (see p. 688). Over fifty species of *Nesoprosopis* fall into structural groups of which one has become parasitic (inquiline) on the others and has lost the special pollen-sweeping apparatus on the front tarsi. Five of these inquiline species have been produced, of course from one original. The three most yellow-spotted species of *Crabro*, which always have a yellow-banded abdomen, are found on Kauai with the yellow-marked *Odyneri*. Two of these Crabros extend to the other islands, or some of the other islands, but one of these, on Oahu, is tending towards

black, while the female is sometimes entirely black. The yellow-banded Crabros on islands other than Kauai are generally found *in the open country* where the yellow-banded *Odyneri* occur." *November 15, 1911.*

It is clear that the colour phenomena exhibited by our Hawaiian Hymenoptera are similar to those seen in other countries (whether in the Hymenoptera or in other orders) where such colour groupings are explained as being associations of inedible species, which are easily recognised by predatory enemies from their similarity of colour. Whether this explanation is true of the Hawaiian case is I think very doubtful, though I do not doubt that a satisfactory explanation of the latter would also explain the others. The Australian Eumenidae, Prosopidae and Fossorial wasps furnish instances very similar to the Hawaiian, and in the same groups, as I have myself observed in the field, in that country.

If we assume that these Colour-groups are formed by processes of natural selection and are indicative of inedibility, we are perplexed as to the immunity of insignificant forms, which do not attain notably iridescent wings or other markings and yet fly round in company with the others and are equally or sometimes more plentiful.

"If the Müllerian theory be correct, *wing coloration* is of paramount importance in the Hawaiian groups. It appears to be very suggestive that most of the clear-winged species of bees and wasps are open-country insects. Of course many of the dark-blue iridescent-winged ones mix with these, but then they are also common in the woods too—I mean individuals of a single dark-winged species are common in both situations.

"There are (with reference to colour of wings) distinct evidences in some Hawaiian Crabronidae, of sexual selection being operative. This again, in connection with Müllerian grouping, might start another distinct line of investigation!" *November 13, 1911.*

The writer collected series of nearly every land-bird on each island and so was able to examine the stomach contents of a large number of birds in all, and the finding of but a single *Mimesa* (in the stomach of the thrush *Phaeornis lanaiensis*) would not tend to show the Hymenoptera, as a favourite food, in any shape or colour. As a matter of fact, an Aculeate Hymenopterous insect (with rare exceptions) is so unlike that of any other Order by its general appear-

ance in life, that one can hardly credit any vertebrate enemy with sense enough to distinguish between Colour-groups of these and without the sense to distinguish the class as a whole.

If Colour-groups in Hymenoptera have arisen as a mark of inedibility, the latter quality can I think have nothing to do with the possession of a sting.*

At one time † I supposed that the Hawaiian Colour-groups might be the result of the action of climatic differences, at least in so far as these groups were special to certain of the islands. This seems very doubtful, for we find the nearest approach to the Colour-group of wasps living in the forests of Kauai, in those living on the driest coasts of Oahu, and quite absent from its very similar forests. In fact a satisfactory explanation of the Colour-groups of Hawaiian Hymenoptera is wanting, and, when found, will no doubt explain some of the similar phenomena elsewhere.

It is interesting to trace the structurally allied forms on different islands and see how their superficial appearance is changed by entering different Colour-groups.

Odynerus eutretus of Hawaii is a black insect with dark-blue iridescent wings; on Maui, it is represented by *O. homoeogaster*, a red-marked wasp; on Kauai, by *O. mimus*, a conspicuously white-banded species. The *obscure-punctatus* group on Hawaii is replaced by the redder species *O. sandwichensis* and its allies on the intermediate islands; on Oahu, the blue iridescence of the wings is lost as well as all the red markings (*O. dubiosus* and allies), while on Kauai, the red markings remain, but the wings are of a shining fuscous (*O. blackburni* and *soror*), as in the Oahuan allies. *Odynerus nigripennis*, ubiquitous over all the other islands, is replaced on Kauai by the equally common, pale-banded *O. radula*, F.

Prosopidae.—All the fifty-three species belong to the single genus *Nesoprosopis* based on the island forms but

* Compare Trans. Ent. Soc., 1904, pp. 645–6.—E. B. P.

† Dr. Perkins is evidently alluding to his paper in Proc. Phil. Soc. Cambridge, vol. ix, Pt. VII, 1897, p. 380, where he argued that the colours are due to "climate or some such cause." He also wrote, November 10, 1911, in reference to the above paragraph in the text :—

"I did not state other reasons against the 'climate' view because I hardly thought it worth considering—there are too many impossibilities in such a view!"

subsequently found to contain a European species, *Prosopis kricchbaumeri*, Först., and later a Chinese one. Thus an Asiatic origin is highly probable. The *Nesoprosopis* are almost the most ubiquitous of any Hawaiian insects.

Crabronidae.—The Hawaiian Crabronidae are represented by eighteen described species, which I have distributed in four genera. All these forms appear to be closely allied, and, as it appears to me, might well be the descendants of one original immigrant yellow-spotted form, allied to the British *Crabro vagus*, L. To this latter there are closely allied species in China, if it does not occur there itself, and for this reason an Asiatic origin for the Hawaiian forms may be suspected. Of the eighteen species, three represent each one a distinct genus, while another genus, *Nesocrabro*, contains four species, so that the greater part of the known forms fall into one genus *Xenocrabro*, of which the others appear to be simply derivatives, and it is to the least remarkable of the Hawaiian species of *Xenocrabro* that the European *Crabro vagus* is most nearly related. None of the other diverse groups of Crabronidae are represented in the Hawaiian Islands.

Some of the species are much and conspicuously marked with yellow on all parts of the body, the yellow markings becoming reduced in others, until, in *X. mandibularis*, Sm., we have an entirely black insect. There is, in the yellow-marked species, much variety in the coloration, and the variation exhibited is often of an interesting character.

C. distinctus, described by Smith from a *Crabro* obtained from Hawaii early in the last century, was at first unknown to me, and I suspected a mistake in the locality. Later on, however, I found that Smith's species is an extreme and rare variety of *C. notostictus*, which is typically a black insect with small yellow thoracic markings. Intermediate specimens between the extremes are much commoner than typical *distinctus*. This brightly marked form has so far only been found at or near the coast, where the intermediate forms also occur, as well as the variety I called *notostictus*. In the mountains in the forest region the latter is predominant and intermediates are rarely met with. From these facts one might suspect that the hot dry climate of the coastal regions was productive of the conspicuously marked varieties. The following considerations make such an explanation improbable. In the genus *Nesocrabro* I

described a species, gaily marked with yellow as *N. bidecoratus*, adding a remark to the effect that "In spite of its extremely distinct appearance I suspect it may prove to be a variety of the following," viz. *N. rubrocaudatus*, Blackb., and Cam. ("Fauna Hawaiiensis," vol. i, Pt. I, Hymenopt. Acul., p. 27, 1899). This now proves to be the case, intermediate varieties having been secured. The variation in this case is even more extreme than in the other, since typical *rubrocaudatus* is an entirely black-bodied insect, whereas the variety *notostictus* of *distinctus* has at least yellow thoracic markings. It is interesting to observe that the markings of the most highly coloured *N. rubrocaudatus* (var. *bidecoratus*) almost entirely resemble those of *Xenocrabro distinctus*. Looking at the localities where these highly marked varieties of *Nesocrabro* occur, we find that, far from living in the hot and dry places, they are found in the wet woods near Kilauea (4,000 ft.), in the still wetter district of Olaa, and other localities of Windward Hawaii. I think that these highly coloured varieties are "reversions" to an ancestral style of coloration, and I believe this is borne out by an examination of the varieties of other Hawaiian species. In these there is a general tendency to blackness of coloration, some few retaining conspicuous yellow markings, while most have these reduced to inconspicuousness or they are entirely absent. *Xenocrabro hawaiiensis* and *fulvicrus*, *Oreocrabro abnormis*, Blackb. and Cam., and *Hylocrabro tumidoventris*, species with normally black abdomen, all become spotted as exceptional and sometimes very rare varieties. Species like *Nesocrabro stygius*, Kirb., and *daemonius*, with immaculate abdomen above, frequently retain yellow pigment spots beneath, where they are concealed from view. Generally speaking yellow markings, especially thoracic, are less easily lost in the female than in the male. The general blackness of the Hawaiian Crabronids, as now manifested, has I think been produced within the islands, and while some still retain more or less the colour of their ancestors the majority have greatly departed therefrom, though many of them in exceptional individuals reproduce that coloration to a greater or less extent. Further, a study of the case cited of *Nesocrabro rubrocaudatus* and *Xenocrabro distinctus* lends strong confirmation to the community of descent that is suggested by the consideration of their structural characters. At least I find it diffi-

cult to understand how two species of these distinct genera can under totally different conditions of climate and environment produce remarkable colour varieties, totally dissimilar from their usual forms, yet almost identical with each other, unless they be reversions to a former style of coloration.

[No further quotations from the Introduction will be found beyond this point, but it has been necessary in the preceding paragraphs to quote from it somewhat extensively, in order that the discussion in the following letters may become clear. After reading the statements reproduced above, I asked Dr. Perkins, among other questions bearing on a possible Müllerian interpretation of the facts, whether the reversion to an ancestral pattern—or more probably the persistence of an ancestral pattern—in the form *distinctus*, might not be associated with the presence of the pale-banded *Odyneri* which are also found in the open country. He replied, Nov. 15, 1911, as follows:—]

X. notostictus, the *black*-bodied form of *distinctus*, seems to be the only form in the forest region where are no pale banded *Odynerus*, except occasional reversional individuals. Typical *distinctus* of Smith is essentially an open country, sublittoral form, but the *notostictus* form may occur with it, and intermediates. There is a number of pale-banded *Odynerus*, belonging to this open country, or sublittoral, and only belonging to this country. Several species of the predominant black group of *Odynerus* are common both in this open country and forest alike. This would be very suggestive to the Müllerian.

The case of var. *bidecoratus* is quite different, for instead of being coastal, it inhabits very wet forest districts, mixed with the typical form but rarer, and probably less widely distributed. Before I knew this, I thought the pale marked Crabronid vars. might be produced by the dryness and heat of the coast region—they average smaller in size also: *bidecoratus* upsets this view.

Müllerians would say that '*notostictus*' persisted in the coastal regions because of the presence of the pale-banded *Odynerus* (or, at least, for the same reason that the latter do, viz. absence of enemies), and would cite the fact that all Crabronids on Kauai are yellow-banded, the black-bodied group of *Odynerus* being absent there. Obviously the colour of the var. *bidecoratus* is quite out of place in wet forests on Hawai, where are no yellow-banded *Odynerus*,

except rare varieties that have reverted to the ancestral pattern. No male form of *bidecoratus* has yet been found, the male *rubrocaudatus* only existing with these so far as is known, and this male is in perfect harmony with the *Odyneri* of the woods. On the Müllerian theory I should say that the more easily changed male of *rubrocaudatus* arrived at a very perfect and stable state of mimetic resemblance to the *Odyneri* of the woods, but that the more conservative female had never reached so perfect a condition—as shown also by its hyaline wings—and that, owing to its conservativeness, it had not reached the stable condition of the male abdominal colouring, when the causes leading to the mimicry (viz. bird attacks) were removed or much abated. I should look on it as a species of which the ancestrally coloured *bidecoratus* form might easily in future times become dominant again.

I have made a crude sketch of a *distinctus* female, from which you can judge how different it appears from an all-black-bodied *notostictus* var., and the brightest female *Nesocrabro rubrocaudatus bidecoratus* has almost a yellow abdomen, the black is so reduced.

[The accompanying drawing of the ♀ *X. distinctus* showed that the following structures and markings are yellow: the pronotal collar, a transverse spot on the scutellum and another on the post scutellum, a curiously shaped spot on the 1st abdominal segment, a band on the 2nd, 4th and 5th, a minute lateral spot on the 3rd, not really visible in a strictly dorsal view. The var. *notostictus* possesses the above-described thoracic markings, but is without the abdominal, although intermediates occur. Another drawing, of the basal abdominal segment of *Nesocrabro rubrocaudatus* var. *bidecoratus*, showed the similar character of the variable yellow spot to that of *X. distinctus*.

Dr. Perkins added:—]

The typical *rubrocaudatus* is entirely black, but in some examples the thorax may have the yellow markings of the var. *bidecoratus*, without any abdominal markings. If abdominal markings are present, thoracic ones are invariably developed.

[Concerning the tendency of the females to lose the white or yellow bands on the abdomen, Dr. Perkins wrote, Nov. 15, 1911:—]

In *Odynerus*, the species of the structural group of *O. sociabilis* and the group of *O. nautarum* have always

the bands more faint or altogether absent in the female. In the Crabronidae the females seem harder to shift from the normal, and I believe that this kind of 'conservatism' is really true of the female sex among insects in general. For instance, in *N. rubrocaudatus*, the male has characteristically dark wings with blue iridescence, but the female has clear wings. In many of the species, the male wings are darker than the female, as though it were hard for the latter to become changed, and this is the same with the thoracic spots, which in three species of *Nesocrabro* with black abdomen are altogether wanting or reduced in size in the male, while they are in two species always, or nearly always, present in the female, and in the third are present in some varieties. They seem to give up these characters with great difficulty.

I should think it much more probable on the Müllerian theory that 'the predominance of female mimicry in butterflies' is due to the necessity of a long life (for egg-laying) for the females, and not to 'a greater female variability in features associated secondarily with sex.'

On the Müllerian theory, I should say that the presence of numerous reversional examples in the Hawaiian species is likely to be due to the fact that nowadays the bird competition has become ineffective. These reversion colours, in *Odynerus* at least, are more often found in males than females; I should say because the females, having once arrived at a stable condition, are less easily changed, i. e. more 'conservative.' There is a war between the greater need to change in the female and the 'conservatism,' doubtless, in producing Colour-groups, just as sexual selection may cause interference. There is not the least doubt that in Hymenoptera generally, the males are of very transitory appearance compared with the females, the difference in length of life often being one of months.

Facts and Arguments for and against Müllerian Mimicry as the Interpretation of the Colour-groups of Hawaiian Aculeates.

[From this point the passages from Dr. Perkins' letters are grouped under heads.]

Nov. 8, 1911.

I have myself for years considered the Batesian theory

of little moment compared with Fritz Müller's: possibly all of Bates's examples are simple Müllerian ones.

Nov. 10, 1911.

I am unable to suggest any explanation whatever for the Colour-groups other than the Müllerian one; but I could not get any definite evidence that this is true. I have examined vast quantities of *young birds* in the islands—they are always present *at all seasons* owing to the equable climate, but what I have examined is nothing to the numbers I have watched at close quarters. Camping entirely alone, as I so often did in untrodden forests—for weeks together during some six years—where the birds had never seen a human being, the young were often so tame, they could even be knocked down with a switch! It was often impossible to shoot a bird, as they would come so close out of curiosity and one could not get away from them, especially young birds.

Nov. 14, 1911.

I should say the present-day Hawaiian birds are very well educated by the parents in the matter of choice of food. It was always a marvel to me why the parents should tend them so long. I have doubtless remarked on it often, but may here quote at random, from "Fauna Haw." I, p. 404, of that common species, *Vestiaria coccinea*, "the yellow, black-spotted young follow the parents sometimes till they are far advanced in their red (i. e. mature) plumage, but they very early learn to obtain nectar for themselves, even at a time when the parents are still feeding them on caterpillars." Again, p. 406, of *Palmeria*: "The young follow the parents often until they have arrived at almost their full plumage, and after they have acquired their full song, but in the winter months these companies are disbanded. In February and March they are generally paired."

I think similar remarks might be made on almost every insectivorous Hawaiian bird, certainly all the common ones. I noted even of the rare and extraordinary *Pseudonestor*, p. 432, "they are unwearying in supplying their *full-fledged* young with food, and when the latter are soliciting this from their parents they form a most comical group."

I do not think any one will ever again see Hawaiian

birds as I did from fifteen to twenty years ago. Some that I found commonly seem now quite extinct, and others greatly reduced in number. It would be almost impossible to duplicate the observations I then made.

Nov. 10, 1911.

What troubles me as to Hymenoptera is, that any bee or wasp in life is so utterly unlike anything else, that the veriest duffer of a bird can hardly mistake it for anything else, and it is clear that in the islands those which remain small in size with no colour of any sort (i. e. no pattern and ordinary wings) are not now eaten and are fully as successful as any belonging to the Colour-groups. Why then on one little island (Oahu) should a lot of species associate themselves in several Colour-groups for protective purposes? It would appear much more advantageous for all to belong to the dominant black-coloured blue-winged group on the one island, as one would say it would be much easier for birds only to have to learn one colour pattern than several. One tasting might do for the whole lot, if they were one colour, but a number of tastings might be necessary for a lot of groups; and then I come back to the old doubt, why is not the fact that all are characteristically Hymenopterous (whatever be the colour) sufficient in itself?

Nov. 15, 1911.

If birds can select between very slight colour variations so as to produce the closest mimetic resemblance, it seems strange that they should not recognise *any* Hymenopterous insect as such quite apart from colour and pattern. That they do recognise Hymenopterous characters other than colour, seems to be proved by a mimetic Australian *Mantispa*. Although superficially quite unlike a Hymenopterous insect, this *Mantispa* is, from its behaviour and attitude, a perfect mimic—in fact the best known to me. No Syrphid with all its wasp-like coloration can approach it.*

* The mimicry of *Mantispa* was observed by W. M. Wheeler in Nebraska (1888), G. A. K. Marshall in Natal (1896), and R. Shelford in Borneo (1898–1900) and Singapore (Trans. Ent. Soc., 1902, pp. 536–7; Proc. Zool. Soc., 1902, pp. 235–7). Both Marshall and Shelford speak of the excellence of the mimicry on the wing. At the same time Shelford's Plate (P. Z. S. 1902, XIX, figs. 22–7), and both his and Wheeler's descriptions show that colour may enter largely into the mimetic resemblance in certain species of *Mantispa*.—E. B. P.

Nov. 13, 1911.

If I could see the very ordinary-looking Hawaiian species —just like those one may see anywhere in the world—at the least disadvantage as compared with those of the special groups, I should have little doubt of the Müllerian theory—though I should still say that in our islands the groups were formed in the past, by causes no longer operative—but the insignificant forms, like many *Nesoprosopis*, are extraordinarily successful in life. Yet we have to admit that those coloured to fit special groups have originated from such forms. The general tendency for the latter to belong to open country and the changed condition of the Avifauna are *the points* that the Müllerian must lay the greatest stress on. I could make the case stronger for him by going into minute detail at considerable length. It would be quite easy to fill a volume with facts concerning these Hymenoptera, dealing with their variations, colours, structures, etc. The true affinities of the species, one to another, becomes very important, when considering the Colour-groups.

Nov. 10, 1911.

With the Hawaiian wasps (*Odynerus*) it must be remembered that, excluding one group of 4 species which are derived from some fairly ancient immigrant from Asia, all the rest are apparently the descendants of *a single very ancient immigrant species*, though by excessive evolutionary change the descendants have now formed distinct genera and structural groups within the islands. There is evidence for the conclusion that the original ancestor was black with yellow bands, such as one now sees all over the world. One must regard all these Colour-groups as having been formed (i. e. started) actually within the islands.

Conditions under which the Hawaiian Colour-groups may have arisen.

Nov. 10, 1911.

If the Müllerian theory is the right one in this case, I am sure that we must look back to a long past time for the formation of the Colour-groups and the causes are no longer operative. I have in the "Fauna Haw.", under "Aves," given a good deal of detailed information about

birds, insects and plants, and have shown how in the birds themselves the causes which developed the weird forms of the peculiar family Drepanididae no longer exist. Nothing but the severest competition for food could ever have produced such birds as *Pseudonestor*, *Heterorrhynchus* and *Chloridops*, the main food of which consists of a single article of diet, to obtain which as a regular diet a very special and grotesque structure has been acquired in each case. Such forms are the tips of twigs in a tree of descent —and they can give rise to nothing further. It might almost be said they are the tips of twigs which, having produced a terminal blossom, themselves die back. A comparatively easy and successful living is possible for a time, but with a slight change of conditions there only remains extinction. They have no chance to adapt themselves to new conditions. It is, I think, noteworthy how often one finds the 'finest' things to be very rare in islands, and I think this is clearly due to the fact that what a systematic student calls 'fine,' is usually a form peculiarly specialised in some particular way, and this means a very particular mode of life. Such 'fine' things are rare, because the conditions suited to their mode of life are few. They are unfortunately the first things to become extinct in Oceanic Islands.

Nov. 8, 1911.

I ought to say I have not finished with the 'colour' question yet, because I have a still more 'general' part than that which I am sending, dealing with 'species formation,' 'variation,' etc., in a general and more comprehensive way, considering the whole fauna together, birds, land-shells, insects and plants.

One who has a wide systematic knowledge of the whole fauna can picture a very different condition of affairs from the present—when the vegetation of the islands formed no true forest, but the islands were covered by a shrubby growth of woody Composites, Lobeliaceae, etc., with few or no trees; when the birds were of less specialised forms like *Himatione* and *Chlorodrepanis* of to-day, with no wonderful developments like *Pseudonestor* and *Heterorrhynchus*, and there were only a few types present, which were numerous in individuals and wandered from shore (where now they are absent) to the mountain tops, and there was a competition for food between individuals, not

to be seen nowadays. There were only a few species of Lepidoptera, mostly Pyralids and Micros., and the wasps, which necessarily came later than these, had no such field for securing food as at present. If the Müllerian theory is correct for these Hawaiian Hymenoptera, then the separation of the Colour-groups began and was developed gradually in past ages and the efficient causes are not observable now.

I stick out absolutely for the formation of all the genera of Drepanid birds within the islands—and what a time it must have taken to produce the extraordinary variety of forms, now seen in this exclusively Hawaiian family! Looking at the birds, one ceases to wonder at the hundreds of species of peculiar Achatinellidae in shells; at the fifty odd species of bees (*Nesoprosopis*) with their wonderful variety; at the 100 or more *Odynerus*, so varied in structure; at the vast genera in various groups of beetles; the (doubtless) hundreds of existing and very varied species of the fly genus *Drosophila*, etc. I doubt whether any but a systematist could rightly appreciate this wonderful fauna, or even a systematist who confined himself to a special group.

It has been a great advantage to me that I was able to work out all the Hymenoptera, Orthoptera and Neuroptera, a large part of the Coleoptera, practically all the Hemiptera (after Kirkaldy) as well as having largely studied many groups of the Lepidoptera and Diptera. Then I made a very large and perfect collection of the birds and wrote upon these also, made special studies in the land-shells, and have a moderate knowledge of the Botany.

Guppy, who wrote on the latter, could never have had his ideas, if he had studied the insects; and the conclusions of specialists like Lord Walsingham, who monographed the Micros., are in my opinion quite untenable (see p. 681).

Nov. 13, 1911.

If the Müllerian theory is true of the Hawaiian wasps, what probably happened is this:—

1. There was a very ancient immigrant *Odynerus* (? whence) which gave rise to the vast majority of the forms now present.
2. It was a black-bodied insect with 2 (or more) narrowish pale abdominal bands.
3. The descendant species of this *Odynerus* may have

formed some Colour-groups (e. g. those with red markings) amongst themselves.

4. A later immigrant species from Asia arrived, a black species with dark blue iridescent wings (like and allied to *nigripennis* of to-day).
5. It became the most abundant and widespread of all species occupying all localities (as *nigripennis* does to-day, excepting in Kauai) on all the islands, except Kauai.
6. On Kauai *only*, *nigripennis* did not remain specifically the same, but gave rise to an equally common, allied species *O. radula*, with two yellow bands.
7. This became *and is* the dominant species on Kauai, and (*a*) may have formed the model for the chief (and almost only) Colour-group on that island, or (*b*) it is likely that the pale-banded group may have previously been a feature of Kauai, and absorbed the immigrant *nigripennis*-like insect (which became also structurally modified), or (*c*) the large series of Kauai forms may have at least developed their dark blue iridescent wings after the pattern of the *nigripennis*-like insect, and it acquired their bands.
8. In the open country of all the islands (excepting Kauai) whether above or below the forest, a large number of species remain, which probably most nearly show the superficial appearance of the original immigrant *Odynerus*.
9. This open country is that which would always (from the nature of the avifauna) have been either devoid of insectivorous birds or very sparsely frequented by them.
10. On Hawaii, the big island, the tendency is decidedly to one uniform condition of blackness and the formation of a single group—the pale-banded forms tending to lose the bands, or having quite lost them in the female sex; the red-marked species having the red marks diminished, faint or dull, as compared with the nearest allied species on the neighbouring islands. Hawaii is very rich in birds.
11. Except on Kauai, the ancestral character of the yellow bands is confirmed by their retention by those species which are least peculiar as compared with foreign forms, and by the fact that almost

any species is, as a very rare variety, liable to produce such a form, the band in such case being often very faint and fine, only found on one segment, sometimes fragmentary, or represented only on the ventral surface, where it is, of course, invisible in life.

12. Though the *nigripennis* group is probably of much later origin in the islands than the other, which it is to be noted has produced within the islands *distinct genera* (*Nesodynerus, Pseudopterocheilus, Chelodynerus*), yet it also is ancient; for it is represented by a highly modified species *O. localis* in Kauai, and by a second distinct one on Oahu, *O. epipseustes*. In *localis* such important structures are modified that much time would be required.
13. Consequently the arrival of the ancestor of the *nigripennis* group may well have happened at a time when the condition of the avifauna was very different.
14. The *nigripennis* group of *Odynerus* might possibly have become much more numerous in species had not the islands been already occupied by a great number of forms developed from the earlier immigration. We may compare the case of the bird family Drepanididae, with that of the later-arriving Meliphagidae.

Importance of the Hawaiian fauna in the study of Evolution.

Nov. 4, 1911.

I believe the Hawaiian islands are for the solving of many most important problems, without any equal elsewhere as at present known. The excessive complications of great continental faunas or continental islands are absent, yet the fauna is itself large enough to present many of the same phenomena. I saw this many years ago and referred to it in my paper on the "Vertebrata" (under the Birds) in the "Fauna Hawaiiensis."

Nov. 13, 1911.

I cannot follow the de Vries people at all. Their mutations and fluctuations are distinctions without any particular difference to me. They know nothing about the instability of the latter. For instance, suppose we

get by selection a melanic form from a pale creature. If it is then placed under exactly similar conditions to those of the parent pale form, it is certainly likely to revert, but if it is, as probably would be the case in nature, maintained for generations, it seems to me the whole life of the creature would be profoundly modified, and germ-cells and many other parts would be affected. Many important external agencies would be changed, absorption of heat, e. g. They seem to expect to see everything revert, because it is known to do so in a limited number of examples and after a few generations.

One of the most important parts of my introduction will deal with insects known to have been introduced. Some of these produce a brood every three weeks or so throughout the year. Is it not remarkable that after years in the islands, and having come from very different countries, we do not find these producing varieties under such new conditions, and after so many generations ?

It seems that it ordinarily takes a great time to start a variable condition, but it does come in the end, for, if we look at the species which are peculiar to the islands, but are comparatively recent arrivals (i. e. not very peculiar and which have not yet given rise to allied species), we see that these are almost always *excessively variable*. Consider how constant are the undersides of *Vanessa atalanta, cardui*, etc., yet our *V. tammeamea*, Esch., allied to these, presents the most remarkable variations constantly. *Hypenodes altivolans*, hardly different from a species found in England, New Zealand, etc., is extraordinarily variable with us, and the same is true of many other Hawaiian species.

Nov. 15, 1911.

I am much impressed with the stability of species for many generations under changed conditions—to which I have referred previously.

Of course a species already in a highly plastic condition would presumably be more likely to exhibit change in a short time. But—

(*a*) In Blackburn's collection (of which I have a large part), formed thirty years ago, variable species exhibited the same varieties then as now.

(*b*) Introduced species from other very diverse countries have not altered after many generations. This

applies to species which are *known* as being plastic outside the islands, i. e. ones which have formed marked varieties or races in countries different from the one whence they were imported to our islands, but which they, no doubt, reached naturally, and at a much more remote period.

From my knowledge of insects generally I should say that species we call very variable are usually really constant in their varieties, i. e. the varieties themselves are of regular occurrence *in nature*—some rarer some commoner, like species. It evidently requires *much time* to alter either species or varieties. What a time it must have taken to produce the eighteen genera of Drepanididae, a family peculiar to the islands! This and the extreme specialisation of so many of the genera seem to point to an ancient excessive competition, unrealisable on present conditions.

I suspect that some day a widespread cause inducing plasticity will be discovered. It must be remembered that many of our commonest imported insects have no enemies at all to keep them constant by selection, but they have not begun to vary *yet*.*

* [The following contribution to this discussion was contained in a letter written by Dr. Perkins from Honolulu, May 20, 1912 :—]

I am astonished after my experience here at the permanency of specific characters. When I see the enormous changes in climate and general conditions produced by the white man's destructive work, and compare examples of all sorts of insects collected to-day with those taken over 75 years ago by old collectors, or 30–40 years ago by Blackburn, I should have expected to have found at least some perceptible difference between the individuals after so many generations (things breed all the year here, many of them average a brood to a month or six weeks).

Again, the conspicuous dominant wasps of the genus *Polistes* introduced nearly half a century ago—more conspicuous and fierce, and more numerous than any *Odyneri*—might have been expected to influence the more plastic of the indigenous species, viz. those which have a coloration that could be easily changed to resemble the new arrivals. In general it appears that an enormous time must be allowed for specific change, unless it occurs abruptly and suddenly. We have lately had a tropical American *Odynerus* introduced here, of quite a different type from our groups; but its appearance could easily be arrived at by some of the native species. This new species (no doubt, imported by man) is already, after a year or so, a most dominant species. Theoretically it should be badly off, as it would be unknown to our endemic birds, etc., and it is not very startling in colour.